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# PHYSIOLOGICAL ECOLOGY - ORIGINAL RESEARCH

## Evidence of variant intra- and interspecific scaling of tree crown structure and relevance for allometric theory

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**Abstract** General scaling rules or constants for metabolic and structural plant allometry as assumed by the theory of Euclidian geometric scaling (2/3-scaling) or metabolic scaling (3/4-scaling) may meet human's innate propensity for simplicity and generality of pattern and processes in nature. However, numerous empirical works show that variability of crown structure rather than constancy is essential for a tree's success in coping with crowding. In order to link theory and empiricism, we analyzed the intra- and inter-specific scaling of crown structure for 52 tree species. The basis is data from 84 long-term plots of temperate monospecific forests under survey since 1870 and a set of 126 yield tables of angiosperm and gymnosperm forest tree species across the world. The study draws attention to (1) the intra-specific variation and correlation of the three scaling relationships: tree height versus trunk diameter, crown cross-sectional area versus trunk diameter, and tree volume versus trunk diameter, and their dependence on competition, (2) the inter-specific variation and correlation of the same scaling exponents ( $\alpha_{h,d}$ ,  $\alpha_{csa,d}$  and  $\alpha_{v,d}$ ) across 52 tree species, and (3) the relevance of the revealed variable scaling of crown structure for leaf organs and metabolic scaling. Our results arrive at suggesting a more extended metabolic theory of ecology which includes

variability and covariation between allometric relationships as prerequisite for the individual plant's competitiveness.

**Keywords** Structural allometry · Euclidian geometry · Metabolic scaling theory · Fractal dimension · Self-thinning

### Introduction

Allometry deals with the size of organisms and its consequences for their shape and functioning. Since the postulation of the allometric equation in the 1930s (Huxley 1932; Teissier 1934), allometry refers to the analysis of logarithmic-transformed bivariate size data by linear regression techniques. Supposing  $x$  and  $y$  quantify the size of plant organs, the growth  $x'$  ( $dx/dt$ ) and  $y'$  ( $dy/dt$ ) is related to the size  $x$  and  $y$  as  $y'/y = \alpha x'/x$ . Better known are the integrated ( $y = a x^{\alpha_{y,x}}$ ) or logarithmic representations ( $\ln y = \ln a + \alpha_{y,x} \times \ln x$ ) which we use subsequently. These equations address the relative change of one plant dimension,  $dy/y$  (e.g., the relative height growth) in relation to the relative change of a second plant dimension  $dx/x$  (e.g., the relative diameter growth). The allometric exponent  $\alpha_{y,x}$  can be perceived as a distribution coefficient for the growth resources between organs  $y$  and  $x$ : when  $x$  increases by 1%,  $y$  increases by  $\alpha_{y,x}\%$ .

Allometric research has largely been driven by the search for overarching, universal allometric exponents. Often, it has been proposed that volume- or mass-related allometric functions scale with exponents based on 1/3 due to the volume dimensionality (von Bertalanffy 1951; Yoda et al. 1963, 1965; Gorham 1979). In the following, we refer to this Euclidian geometric scaling, which assumes, e.g.,

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$\alpha_{h,d} = 1$ , and  $\alpha_{v,d} = 3$ , and  $\alpha_{v,h} = 3$  as geometric scaling theory (GST). More recently, West et al. (1997, 2009), Enquist et al. (1998, 2009), and Enquist and Niklas (2001) presented a critically debated (Kozłowski and Konarzewski 2004; Reich et al. 2006; Pretzsch 2010) general explanation of allometric scaling with exponents to be derived from 1/4 based on the fractal network of transportation systems in organisms. In the following, we refer to the latter as metabolic scaling theory (MST). It assumes the following common scaling relationships for allometric ideal plants:  $\alpha_{h,d} = 2/3 = 0.\overline{6}$ , and  $\alpha_{v,d} = 8/3 = 2.\overline{6}$ ,  $\alpha_{v,h} = 12/3 = 4$  (West et al. 2009). Many empirical studies frequently use these common geometric or fractal scaling exponents as a starting point and null hypothesis for revelation of species-specific deviations from GST and MST (Zeide 1987; Niklas 1994; Pretzsch 2006).

The metabolic scaling theory (MST) provides a promising synthesis for the functioning and structure of plants from organ to ecosystem level (Enquist et al. 1998; West et al. 2009). MST is built on rather simple assumptions on individual metabolism; MST predicts growth and even morphology of trees and stands (Enquist et al. 2009). The mainstay of MST, the scaling between leaf mass, ml, and total plant biomass, mt, is widely held to follow the 3/4 power scaling rule (Niklas 2004)

$$ml \propto mt^{3/4}. \quad (1)$$

However, Price et al. (2009, 2010) suggest a significant variability between species so that MST appears overly simplistic when confronted with empirical findings. MST further generalizes the morphological scaling, i.e. it also assumes rather invariant scaling relationships for the holding structure of the leaf organs. In view of the morphological plasticity found by many studies (Pretzsch 2006; Purves et al. 2007; Pretzsch and Mette 2008; Price et al. 2010), morphological constant scaling as assumed by West et al. (2009) may be useful as a first assumption. This enable a simple transition from scaling of metabolism to scaling of structure and paves the way to the stand level, where structure means space and resource occupation. However, stable metabolic scaling, as predicted by MST, and variable scaling of crown structure, as found in many empirical studies, is not a contradiction. Maybe morphological plasticity is even a requirement for holding trees on a rather stable leaf mass–plant mass trajectory.

We demonstrate this thought by the scaling exponent  $\alpha_{cv,v}$  of crown volume, cv, versus tree volume, v. On closer inspection, it is possible to separate  $\alpha_{cv,v}$  into the three components,  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$  and  $\alpha_{v,d}$  which result in  $\alpha_{cv,v} = (\alpha_{h,d} + \alpha_{csa,d})/\alpha_{v,d}$ . First, it is considered that scaling between tree height, h, and trunk diameter, d, is  $h \propto d^{\alpha_{h,d}}$ . According to McMahon and Kronauer (1976), crown

length, cl, is predicted to be proportional to height yielding the prediction  $h \propto cl \propto d^{\alpha_{h,d}}$ . Secondly, it is considered, that crown cross-sectional area, csa, scales in relation to trunk diameter like  $csa \propto d^{\alpha_{csa,d}}$ . As crown volume is the product of crown length and crown cross-sectional area ( $cv = cl \text{ csa}$ ), this results in  $cv \propto d^{(\alpha_{h,d} + \alpha_{csa,d})}$ . Thirdly, it is assumed that  $v \propto d^{\alpha_{v,d}}$ , so that  $d \propto v^{1/\alpha_{v,d}}$ . Combination of these three components yields

$$cv \propto v^{(\alpha_{h,d} + \alpha_{csa,d})/\alpha_{v,d}}, \quad (2)$$

and shows that  $\alpha_{cv,v} = (\alpha_{h,d} + \alpha_{csa,d})/\alpha_{v,d}$ . MST assumes common scaling relationships for allometric ideal plants, e.g.,  $\alpha_{h,d} = 2/3$ ,  $\alpha_{csa,d} = 4/3$ ,  $\alpha_{v,d} = 8/3$ , and as basic assumption according to Eq. (1)  $\alpha_{cv,v} = 3/4$  (West et al. 2009). Insertion of the general scaling exponents for an allometric ideal plant into Eq. (2) yields  $\alpha_{cv,v} = (2/3 + 4/3)/(8/3) = 3/4$ . However,  $\alpha_{cv,v} = 3/4$  could also result from diverging components, e.g.,  $\alpha_{cv,v} = (1/3 + 5/3)/(8/3) = 3/4$ . Deviation in scaling of structure from the allometric ideal plant is not inevitably a contradiction to the core assumption of the 3/4 scaling of MST (Eq. 1). On the other hand, when parts of the crown developments correspond with MST, that does not indicate inevitably that the scaling on whole tree level also corresponds with MST, because covariation of other allometric relationships can cancel, compensate, or enhance the scaling on tree level.

This study will not continue the questionable hunting for overarching scaling exponents, falsification or confirmation of GST or MST. By exploiting a unique dataset, we rather draw attention to (1) the intra-specific variation and correlation of the three scaling relationships; tree height versus trunk diameter, crown cross-sectional area versus trunk diameter, and tree volume versus trunk diameter, and their dependence on competition, (2) the inter-specific variation and correlation of the same scaling exponents ( $\alpha_{h,d}$ ,  $\alpha_{csa,d}$  and  $\alpha_{v,d}$ ) across 52 tree species, and (3) the relevance of the revealed variable scaling of crown structure for a plastic holding structure for the leaf organs and metabolic scaling.

## Materials and methods

### Data source: long-term experimental plots

One basis of this study is data from long-term experimental plots in Bavaria, Germany, which have been under survey since 1870 and belong to the world's oldest network of experimental plots in forests (for details, see Appendix S1). For this study, 84 plots in pure stands of Norway spruce ( $n = 36$ ), European beech ( $n = 23$ ), and sessile oak ( $n = 25$ ) were selected. By including these three tree

species, the data cover shade-tolerant species (European beech) as well as light-demanding species (sessile oak). The selection of the experimental plots includes a broad range of site conditions, which is reflected by the site index (see Appendix S13) which ranges from 22.0 to 44.9 m height at age 100 years. In order to consider the species' crown variability, completely unthinned to heavily thinned plots were selected, allowing for the study of a range of close to wide spacing conditions. The spacing is quantified in terms of the stand density index values (Reineke 1933; see Appendix S13), which span from 266 (solitary tree growth) to 1,967 trees per hectare (self-thinning conditions).

For the artificially established stands, tree age was derived from the time since establishment. For the naturally established stands, tree age was measured by ring analyses on increment cores. Diameter at breast height was measured with girth tape. Tree height and height of the crown base (base of the crown's lowest primary branch) were measured with the inclinometer Christenmeter (geometrical principle) until the 1960s, thereafter replaced by the Blume Leiss (trigonometrical principle), which was in use until the 1990s, before being replaced by the Vertex (trigonometrical principle with laser beam-based distance measurement). In the planted stands, stem co-ordinates were known from planting plans; in the stand which were seeded or established by natural regenerations stem co-ordinates were originally measured by tape, a method which was replaced by the theodolite Leica TC500 during the 1990s. Measurements of crown radii were carried out with the biritz + hatzi<sup>TM</sup> optical perpendicular instrument in eight cardinal compass directions (N, NE,...NW). Crown cross-sectional area  $c_{sa} = \bar{r}^2 \pi$  was then calculated using the quadratic mean radius  $\bar{r} = \sqrt{(r_1^2 + r_2^2 + \dots + r_8^2)/8}$ . For the estimation of the total above ground tree volume,  $v$ , we applied species-specific volume functions, which calculate the volume from height to diameter (see Appendix S2 and S3).

Altogether, the dataset comprises about 10,000 observations of Norway spruce ( $n = 4,375$ ), European beech ( $n = 2,006$ ), and sessile oak ( $n = 3,358$ ) (Appendix S4). Tree diameter,  $d$ , ranges from 3.0 to 103.4 cm, tree height,  $h$ , from 4.7 to 46.3 m, crown cross-sectional area,  $c_{sa}$ , from 0.4 to 318.4 m<sup>2</sup>, and above-ground tree volume,  $v$ , from 0.002 to 20.042 m<sup>3</sup>. Tree cover index,  $tci$ , and stand density index,  $sdi$ , quantify the vertical and lateral competitive status of the trees. They span values of  $tci = 0$ –0.82 and  $sdi = 30$ –1,161 (see “Determination of a tree's competitive status”).

Data source: forestry yield tables

Forest yield tables are derived from long-term experimental plots and present stand development in tabular form

(Pretzsch 2009). By reporting static stand values like mean diameter, standing volume, and volume increment over the period of stand development, yield tables accumulate empirical knowledge from long-term observations (see Appendix S13). While they are frequently used as forest planning tools, their underlying data are seldom applied to allometric analysis (Zeide 1987).

In this study, 126 yield tables of 52 species, 30 of angiosperm, and 22 of gymnosperm taxonomy (Appendix S5) were analyzed. Species included the genera *Abies*, *Acer*, *Alnus*, *Betula*, *Carpinus*, *Castanea*, *Cunninghamia*, *Eucalyptus*, *Fagus*, *Fraxinus*, *Juglans*, *Larix*, *Nothofagus*, *Picea*, *Pinus*, *Populus*, *Prunus*, *Pseudotsuga*, *Quercus*, *Robinia*, *Shorea*, *Thuja*, and *Tilia* (Appendix S7). From these yield tables, we derived, for the average tree of the stand, its mean diameter,  $\bar{d}$ , height,  $\bar{h}$ , volume,  $\bar{v}$ , by dividing total stand volume,  $V$ , by stem number,  $N$ , ( $\bar{v} = V/N$ ), growing area,  $\bar{g}_a$ , and growing space,  $\bar{g}_s$  ( $\bar{g}_s = \bar{h} \bar{g}_a$ ). For explanation of mean height, mean diameter, and growing space, see Appendix S13. In order to assure that crown cross-sectional area,  $\bar{c}_{sa}$ , scales proportionally to growing area,  $\bar{g}_a$ , ( $\bar{c}_{sa} \propto \bar{g}_a$ ), exclusive yield tables covering self-thinning conditions or light and moderate thinning regimes were taken into account. Light and moderate thinning keeps a stand's canopy permanently in such a kind of structure that the tree crowns just touch but do not overlap each other. By definition of the silvicultural treatment standards (Pretzsch 2009, pp. 156–160), these stands have a canopy density which fulfills the requirement for deducing mean tree growing area,  $\bar{g}_a$ , from the 1-ha (10,000 m<sup>2</sup>) large reference area of the yield tables and total stem number,  $N$ , ( $\bar{g}_a = 10,000/N$ ). In the following, the notation  $\bar{c}_{sa}$  is used instead of  $\bar{g}_a$ . Based on the assumption that  $cl \propto h$  and  $c_{sa} \propto g_a$ , we can relate  $\bar{c}_{sa}$  to  $\bar{g}_s$  as  $\bar{c}_{sa} \propto \bar{g}_s$ .

#### Determination of a tree's competitive status

As individual tree size attributes and tree positions are available for all plots, the competitive status of each tree can be determined. Stand characteristics are analyzed for each individual tree  $k$  within a circle of radius  $r$ , with the assumption that most of a tree's relevant competitors are located within a certain distance of its mean crown diameter. Mean crown diameter itself was estimated based on the diameter and height of tree  $k$ , using empirical functions by Pretzsch and Biber (2010) (Appendix S6). In order to characterize the vertical position, the tree cover index,  $tci$ , (Appendix S7) was employed. The first step in deriving  $tci$  was to obtain the maximum tree height,  $h_{max}$ , within a radius  $r_k$ . By setting the height of tree  $k$  in relation to  $h_{max}$ , the  $tci_k$  variable can be calculated from  $tci_k = 1 - h_k/h_{max}$ .

**Table 1** Intra-individual scaling exponents  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ ,  $\alpha_{v,d}$ , and  $\alpha_{cv,v}$  observed on the long-term plots of Norway spruce and European beech

Species	Characteristics	$\alpha_{h,d}$	$\alpha_{csa,d}$	$\alpha_{v,d}$	$\alpha_{cv,v}$
General	Expected				
	Geometric similitude	1.00	2.00	3.00	1.00
	Allometric ideal plant	0.67	1.33	2.67	0.75
	Norway spruce	Observed			
	<i>n</i> (measurements)	3,668	4,230	3,668	3,528
	<i>n</i> (individuals)	2,566	3,001	2,566	2,425
	Mean $\pm$ SE	0.63 ( $\pm 0.006$ )	1.50 ( $\pm 0.017$ )	2.56 ( $\pm 0.004$ )	0.80 ( $\pm 0.006$ )
	95% CI limits	0.62–0.64	1.47–1.54	2.55–2.57	0.79–0.82
	Min $\alpha^k$ –max $\alpha^k$	0.37–0.78	0.98–2.07	2.41–2.66	0.65–0.91
	Coeff var.	0.57	0.74	0.10	0.46
	European beech	Observed			
	<i>n</i> (measurements)	1,446	1,960	1,446	1,400
	<i>n</i> (individuals)	1,058	1,509	1,058	1,015
Scaling exponents expected under geometric similitude and predicted for the allometric ideal plant serve as reference	Mean $\pm$ SE	0.55 ( $\pm 0.007$ )	1.19 ( $\pm 0.021$ )	2.54 ( $\pm 0.006$ )	0.77 ( $\pm 0.012$ )
	95% CI limits	0.53–0.56	1.15–1.23	2.53–2.55	0.75–0.80
	Min $\alpha^k$ –max $\alpha^k$	0.50–0.58	0.87–1.40	2.49–2.59	0.61–0.89
	Coeff var.	0.51	0.77	0.09	0.58
	Sessile oak	Observed			
	<i>n</i> (measurements)	2,698	3,004	2,698	2,344
	<i>n</i> (individuals)	1,993	1,852	1,993	1,705
	Mean $\pm$ SE	0.60 ( $\pm 0.003$ )	1.60 ( $\pm 0.016$ )	2.63 ( $\pm 0.002$ )	0.82 ( $\pm 0.006$ )
	95% CI limits	0.59–0.61	1.57–1.63	2.63–2.64	0.81–0.83
	Min $\alpha^k$ –max $\alpha^k$	0.47–0.71	0.99–1.87	2.54–2.71	0.52–0.96
	Coeff var.	0.25	0.5	0.04	0.34

Scaling exponents expected under geometric similitude and predicted for the allometric ideal plant serve as reference

$\alpha_{h,d}$  scaling of tree height *h*, versus trunk diameter *d*;  $\alpha_{csa,d}$  crown cross-sectional area *csa*, versus trunk diameter *d*;  $\alpha_{v,d}$  tree volume *v*, versus trunk diameter *d*;  $\alpha_{cv,v}$  crown volume *cv*, versus trunk volume *v*

Higher  $tc_{ik}$  values indicate a suppression of tree *k*. The lateral restriction of tree *k* is quantified by the density index  $sdi_k$  on the same plot around tree *k* which was used for  $tc_i$  estimation (Appendix S7).  $Sdi_k$  is defined as the equivalent trees per hectare at a quadratic mean diameter of 25 cm and is formulated as  $sdi_k = N_{obs}(25/\bar{d})^{\alpha_{N,\bar{d}}}$  in accordance with Reineke (1933), where  $N_{obs}$  is the tree number and  $\bar{d}$  is the quadratic mean diameter on the respective concentric plot with radius  $r_k$ . For calculation of the  $sdi_k$ , generalized  $\alpha_{N,\bar{d}} = -1.605$  by Reineke (1933) was applied (see Appendix S13).

### Scaling of structure

For all analysis, the allometric exponent  $\alpha$  was predicted by ln–ln regression straight lines of the form  $\ln y = \ln \beta + \alpha \ln x$ , where *x* and *y* denote the size of an organ or body part of interest,  $\beta$  is the normalization constant and  $\alpha$  the allometric scaling exponent.

On the individual tree scale, where data from long-term plots are partially auto-correlated due to several

observations taken on the same subjects (see Table 1), linear mixed effect models of the type:  $\ln y_{jk} = \ln \beta + \alpha \ln x_{jk} + a_k \ln x_{jk} + \varepsilon_{jk}$  with individual = *k* and time = *j* as an individual-specific random effect  $a_k$  on slope were applied (Pinheiro and Bates 2000). Thus, confidence intervals of the fixed parameters are realistic because the intra-individual observations are treated as dependent, while the individuals themselves are considered to be independent from each other. The random effect  $a_k$  and the error  $\varepsilon_{jk}$  was assumed to be normally distributed with mean = 0 and constant variance. The fixed-effect coefficient  $\alpha$  represents the average allometric relationship between *x* and *y* and is to be seen as the species-specific mean scaling exponent. As the intra-specific variation is captured by  $a_k$  the method additionally allowed to extract an local subject-specific allometric coefficient  $\alpha^k$  for each tree *k* by combining the fixed-effect estimate and the random effect. The analysis is focusing on this local exponent as it captures the variation in form and development. The mean of  $\alpha^k$  equals  $\alpha$  and is used for comparisons between species. For fitting the models, the function *lmer* from the

R software package ‘lme4’ (R Development Core Team 2009; Bates et al. 2011) was chosen. Different combinations of random effect coding were tested and the approach with random effect  $a_k$  on slope yielded the most plausible results. The default method of restricted maximum likelihood (REML) was used for parameter estimation (Pinheiro and Bates 2000).

For allometric analysis of cross section data on stand level (see yield table data, S5), scaling exponents  $\alpha_{\bar{y},\bar{x}}$  were estimated by Standardized Major Axis (SMA) regression, also known as Reduced Major Axis (RMA) regression, using the R software package ‘smatr’ (see Sackville Hamilton et al. 1995; Warton et al. 2006; R Development Core Team 2009). Linear regressions were fitted for each yield table and species separately. Then, 95% confidence intervals were calculated for species groups using the allometric exponents  $\alpha$  depicted from each single regression. SMA minimizes both the  $x$  and the  $y$  errors and was therefore most appropriate for the purpose of extracting the slope of the regression straight line of best fit.

Analyses focusing on the dependency of the scaling exponents  $\alpha_{h,d}^k$  and  $\alpha_{csa,d}^k$  from tci and sdi were performed using OLS regressions with tci and sdi as independent variables. Alternative regression designs with predictor variables included only as first-order effects (linear) and additionally as second-order effects (quadratic) were tested. Based on AIC and BIC ranking (Akaike 1974; Schwarz 1978), the final model design of  $\alpha_{h,d}^k$  and  $\alpha_{csa,d}^k$  for spruce and beech yielded tci and sdi as first-order effects and tci as second-order effect.

The subscripts of the allometric exponent  $\alpha$  indicate which variables are addressed. Note that when reporting

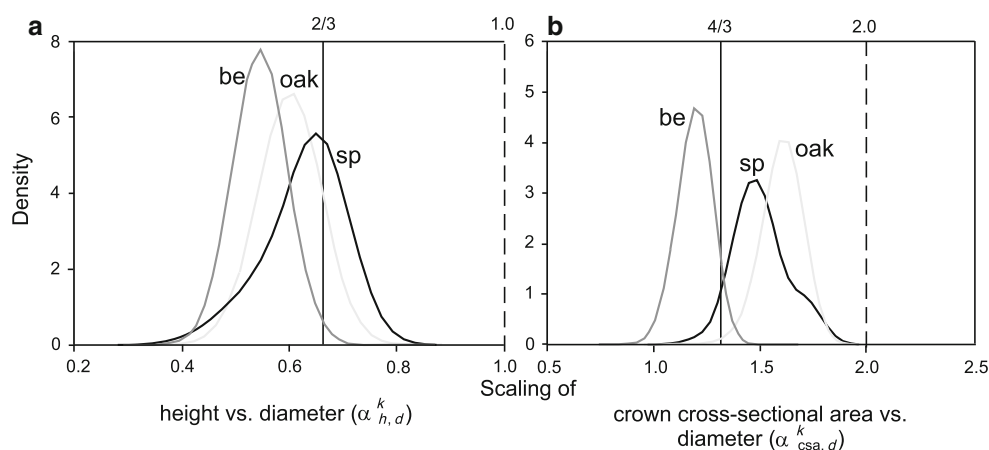
$\alpha_{y,x}$ , the exponent is calculated on the individual tree scale, whereas  $\alpha_{\bar{y},\bar{x}}$  refers to mean tree values (see Appendix S12). All reported allometric exponents are estimated directly on the basis of the individual tree or mean tree data; that also applies to the estimation of the scaling exponent for crown volume versus tree volume,  $\alpha_{cv,v}$ . In Eq. (2), we derived  $\alpha_{cv,v}$  from its components  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ , and  $\alpha_{v,d}$  for showing the theoretical relationships. However, the subsequently reported  $\alpha_{cv,v}$  exponents were estimated empirically on the basis of the individual tree data, in order to avoid error propagation. This means that for the calculation of  $cv$  and  $v$ , height, crown cross-sectional area and diameter, respectively, were directly used as measured including all stochastic variation like measurement errors, etc.

## Results

### Intra-specific variability and covariation

Figure 1 shows the density distribution for the intra-individually derived allometric exponents  $\alpha_{h,d}^k$  and  $\alpha_{csa,d}^k$  which represent the vertical and lateral crown expansion of Norway spruce, European beech, and sessile oak in pure stands (data base, see Table 1). The graph reveals that both exponents have a broad variation, that the three species differ considerably concerning these two scaling exponents, and that there is no clear correspondence with metabolic scaling (solid vertical lines) or Euclidian geometric scaling (broken vertical lines).

The individual scaling components of Eq. 2 ( $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ , and  $\alpha_{v,d}$ ) as well as the overall exponent  $\alpha_{cv,v}$  reveal for all



**Fig. 1** Density distribution of observed scaling exponents **a**  $\alpha_{h,d}^k$  and **b**  $\alpha_{csa,d}^k$  for Norway spruce (*sp*), European beech (*be*) and sessile oak (*oak*) based on individual tree measurements on long-term experimental plots in pure stands. Expected scaling exponents for an allometric ideal plant according to metabolic scaling theory and

Euclidian geometric similitude are represented by *solid* and *broken bars*, respectively  $\alpha_{h,d}^k$ , scaling of individual tree height  $h$ , versus individual tree diameter  $d$ ;  $\alpha_{csa,d}^k$ , individual tree crown cross-sectional area  $csa$ , versus individual tree diameter  $d$

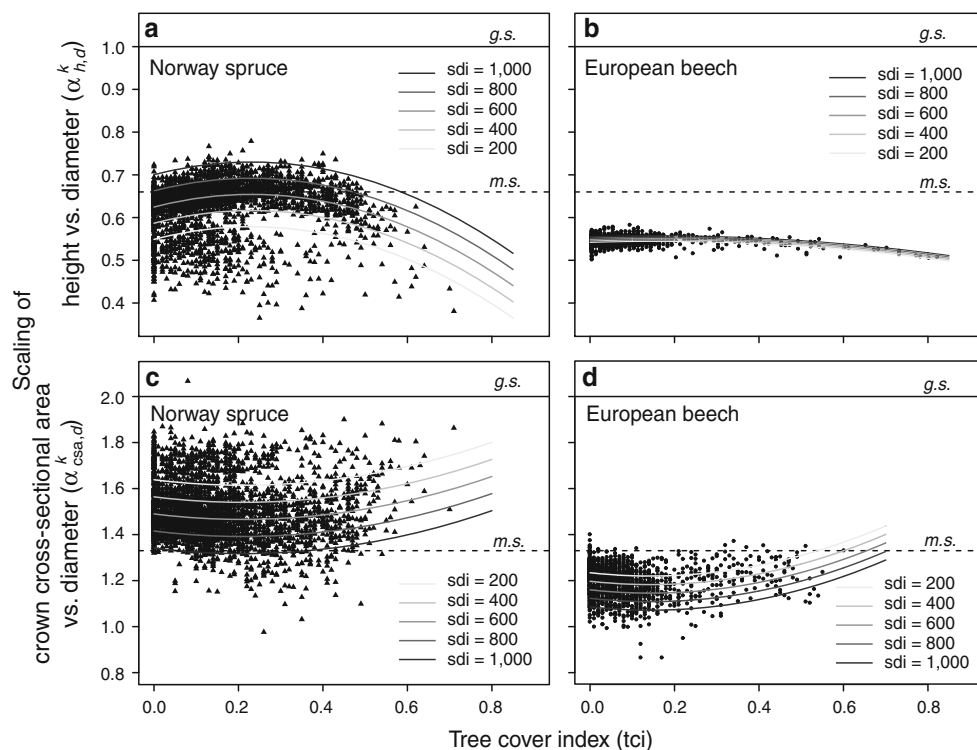


three species an intra-specific variation indicated by means, 95% CIs, and coefficients of variation (Table 1).

A large proportion of the scaling exponents' variation results from vertical and lateral crown restriction quantified by the tree cover index, *tci*, and stand density index, *sdi*. The combined effect of *tci* and *sdi* on  $\alpha_{h,d}^k$  (Fig. 2a, b) and  $\alpha_{csa,d}^k$  (Fig. 2c, d) becomes evident by fitting the following model to the data:  $\alpha_{h,d}^k = 0.511 + 0.000189 \text{ sdi} + 0.258 \text{ tci} - 0.558 \text{ tci}^2$  ( $r^2 = 0.35$ ,  $n = 2,566$ ,  $p < 0.001$ ) and  $\alpha_{csa,d}^k = 1.713 - 0.000372 \text{ sdi} - 0.227 \text{ tci} + 0.537 \text{ tci}^2$  ( $r^2 = 0.28$ ,  $n = 3,001$ ,  $p < 0.001$ ) for Norway spruce and  $\alpha_{h,d}^k = 0.539 + 0.000017 \text{ sdi} + 0.030 \text{ tci} - 0.096 \text{ tci}^2$  ( $r^2 = 0.16$ ,  $n = 1,058$ ,  $p < 0.001$ ) and  $\alpha_{csa,d}^k = 1.271 - 0.000186 \text{ sdi} - 0.201 \text{ tci} + 0.701 \text{ tci}^2$  ( $r^2 = 0.20$ ,  $n = 1,509$ ,  $p < 0.001$ ) for European beech. With increasing competition trees first slightly enhance and then strongly reduce their height growth. With increasing *tci*,  $\alpha_{csa,d}^k$  increases as trees develop shade habitus. Thus,  $\alpha_{h,d}^k$  and  $\alpha_{csa,d}^k$  react contrarily to an increase of competition reflected by the tree cover index, *tci*. While the former follows a concave (seen from below) reaction pattern,

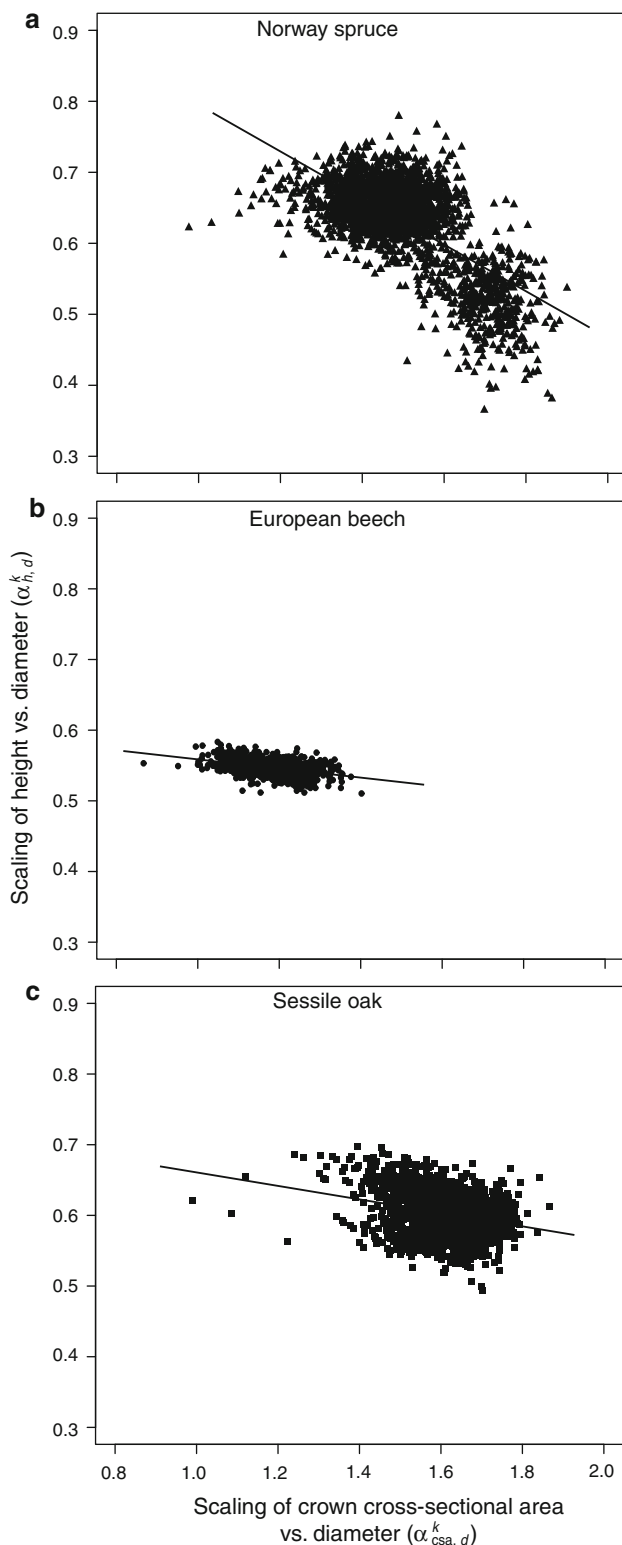
the latter shows a convex course. The effect of stand density on the two scaling exponents is also inversely related: when stand density increases ( $\text{sdi} = 200 \dots 1,000$ ),  $\alpha_{h,d}^k$  increases, but  $\alpha_{csa,d}^k$  declines.

The more trees foster their vertical extension, the less they grow in width. This tradeoff between crown height and width is reflected by the correlation coefficients of  $r = -0.68$  for Norway spruce,  $-0.44$  for European beech and  $-0.27$  for sessile oak reflect (Fig. 3, Table 2). This correlation between the components of Eq. 2  $\alpha_{cv,v} = (\alpha_{h,d}^k + \alpha_{csa,d}^k)/\alpha_{v,d}$  contributes to the stabilization of the scaling of crown volume versus tree volume  $\alpha_{cv,v}$  between 0.79–0.82 for Norway spruce, 0.75–0.80 for European beech, and 0.81–0.83 for sessile oak (Table 1). The wider the lateral extension, the smaller the vertical reach and vice versa. With other words, even, when both,  $\alpha_{h,d}^k$  and  $\alpha_{csa,d}^k$  seen individually differ considerably from  $\alpha_{h,d}^k = 2/3$  and  $\alpha_{csa,d}^k = 4/3$  (predicted by MST), the overall allometry of the crown  $\alpha_{cv,v}$  may remain rather stable, as deviations from MST cancel each other. That does not mean that  $\alpha_{cv,v} = 3/4$  but that  $\alpha_{cv,v} \cong \text{const.}$  on a species-specific level.



**Fig. 2** Dependency of inter-individual allometric scaling exponents on competition displayed for  $\alpha_{h,d}^k$  for **a** Norway spruce and **b** European beech and  $\alpha_{csa,d}^k$  for **c** Norway spruce and **d** European beech. Horizontal lines represent scaling expected for geometric similitude (solid line) and allometric ideal plant (dashed line). Lines are ordinary least square regression curves including *tci* and *sdi* as

covariates. All shown OLS-fits are significant improvements over linear fits based on AIC and BIC. In case of the lines in the plots, *sdi* has been set to values between 200 and 1,000.  $\alpha_{h,d}^k$ , scaling of height versus trunk diameter;  $\alpha_{csa,d}^k$ , scaling of crown cross-sectional area versus trunk diameter; *tci*, tree cover index; *sdi*, stand density index



**Fig. 3** Correlation between  $\alpha_{h,d}^k$  and  $\alpha_{csa,d}^k$  which amounts to **a**  $r = -0.68$  for Norway spruce, **b**  $r = -0.44$  for European beech and **c**  $r = -0.27$  for sessile oak. Shown are the intra-individual scaling exponents. The statistics of the linear regression lines are shown in Table 2.  $\alpha_{h,d}^k$ , scaling of height  $h$ , versus trunk diameter  $d$ ;  $\alpha_{csa,d}^k$ , scaling of crown cross-sectional area  $csa$ , versus trunk diameter  $d$

### Differences in scaling of structure between species

The three species analyzed on long-term plots differ considerably in the mean observed scaling exponents  $\alpha_{h,d}$  and  $\alpha_{csa,d}$  (see Fig. 1; Table 1). Sessile oak appears to be highly variable in lateral expansion but rather limited in vertical plasticity. Norway spruce's strength lies rather in its vertical plasticity and that of European beech in its lateral spread. Analyses of variance (not shown) showed significant ( $p < 0.001$ ) differences between the three species concerning all scaling exponents of their crown structure. However, the scaling relations  $\alpha_{cv,v}$  are less distinct between the species than those of  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ , and  $\alpha_{v,d}$  (Table 1).

The frequency distribution of the observed scaling exponents at stand level across 52 species based on 126 yield tables revealed a high variation of  $\alpha_{csa,d}$  and  $\alpha_{cv,v}$ , which encompass lateral crown expansion. In contrast, the variance of  $\alpha_{h,d}$  and  $\alpha_{v,d}$ , which represent scaling of the stem, is more narrow (Fig. 4, notice the different scales of the abscissa.). The means and the 95% CIs (black vertical bar with gray peripheral area) amount to  $\alpha_{h,d} = 0.830 \pm 0.017$ ,  $\alpha_{csa,d} = 1.458 \pm 0.030$ ,  $\alpha_{v,d} = 2.820 \pm 0.036$ , and  $\alpha_{cv,v} = 0.817 \pm 0.011$  (Appendix S8). For the group of gymnosperm species, the observed scaling exponents,  $\alpha_{h,d} = 0.903 \pm 0.021$ ,  $\alpha_{csa,d} = 1.431 \pm 0.032$ ,  $\alpha_{v,d} = 2.887 \pm 0.047$ , and  $\alpha_{cv,v} = 0.837 \pm 0.012$ , are 3–23% greater than those for the angiosperm species with  $\alpha_{h,d} = 0.733 \pm 0.022$ ,  $\alpha_{csa,d} = 1.410 \pm 0.055$ ,  $\alpha_{v,d} = 2.732 \pm 0.054$ , and  $\alpha_{cv,v} = 0.791 \pm 0.091$  (Appendix S9, S10). Both groups are significantly different in  $\alpha_{h,d}$ , whereas the confidence intervals of the other allometric exponents overlap. Analysis of the correlation between the components of  $\alpha_{cv,v} = (\alpha_{h,d} + \alpha_{csa,d})/\alpha_{v,d}$  (Eq. 2) reflects the high plasticity by which trees crowns can occupy space. Pearson's correlation reveals a trade-off between  $\alpha_{h,d}$  and  $\alpha_{csa,d}$  indicated by  $r = -0.36^{***}$ . In contrast,  $\alpha_{h,d}$  is positively correlated to  $\alpha_{v,d}$  ( $r = 0.36^{***}$ ), and  $\alpha_{csa,d}$  is also positively correlated to  $\alpha_{v,d}$  ( $r = 0.15$ ) (Appendix S11). The trade-off between  $\alpha_{h,d}$  versus  $\alpha_{csa,d}$  is mainly responsible for the vertical and lateral crown plasticity. Across all species,  $\alpha_{h,d}$  values range from 0.5 to 1.5 and  $\alpha_{csa,d}$  from 0.2 to 2.4 with the gymnosperm tree species (triangles) concentrated in the upper half of the scatterplot and the angiosperms (circles) in the lower (Fig. 5). OLS regression yielded  $\alpha_{h,d} = 1.131 - 0.206 \alpha_{csa,d}$  ( $n = 126$ ,  $p < 0.001$ ,  $r^2 = 0.13$ ,  $F_{1,124} = 18.97$ ) represented by the straight line. For the two further components of Eq. 2 OLS-regression yielded  $\alpha_{csa,d} = 1.108 + 0.124 \alpha_{v,d}$  ( $n = 126$ ,  $p < 0.10$ ,  $r^2 = 0.02$ ,  $F_{1,124} = 2.81$ ), and  $\alpha_{h,d} = 0.348 - 0.171 \alpha_{v,d}$

**Table 2** Correlation between intra-individual scaling exponents of Norway spruce, European beech, and sessile oak

Species	Characteristics	$\alpha_{h,d}^k \times \alpha_{csa,d}^k$	$\alpha_{h,d}^k \times \alpha_{v,d}^k$	$\alpha_{csa,d}^k \times \alpha_{v,d}^k$
Norway spruce	OLS regression			
	$a_0 (\pm SE)$	1.12 ( $\pm 0.011$ )	−3.03 ( $\pm 0.023$ )	6.43 ( $\pm 0.127$ )
	$a_1 (\pm SE)$	−0.33 ( $\pm 0.007$ )	1.43 ( $\pm 0.009$ )	−1.92 ( $\pm 0.049$ )
	$N$	2,425	2,566	2,425
	$p$ value	$p < 0.001$	$p < 0.001$	$p < 0.001$
	$R^2$	0.461	0.904	0.385
	Pearson correlation			
	$r$	−0.68	+0.95	−0.62
	$p$ value	$p < 0.001$	$p < 0.001$	$p < 0.001$
European beech	OLS regression			
	$a_0 (\pm SE)$	0.62 ( $\pm 0.005$ )	−1.35 ( $\pm 0.016$ )	6.64 ( $\pm 0.362$ )
	$a_1 (\pm SE)$	−0.06 ( $\pm 0.004$ )	0.75 ( $\pm 0.006$ )	−2.15 ( $\pm 0.143$ )
	$N$	1,015	1,058	1,015
	$p$ value	$p < 0.001$	$p < 0.001$	$p < 0.001$
	$R^2$	0.192	0.930	0.183
	Pearson correlation			
	$r$	−0.44	+0.99	−0.43
	$p$ value	$p < 0.001$	$p < 0.001$	$p < 0.001$
Sessile oak	OLS regression			
	$a_0 (\pm SE)$	0.76 ( $\pm 0.014$ )	−2.91 ( $\pm 0.014$ )	4.32 ( $\pm 0.224$ )
	$a_1 (\pm SE)$	−0.10 ( $\pm 0.008$ )	1.33 ( $\pm 0.005$ )	−1.03 ( $\pm 0.085$ )
	$N$	1,705	1,993	1,705
	$p$ value	$p < 0.001$	$p < 0.001$	$p < 0.001$
	$R^2$	0.074	0.969	0.080
	Pearson correlation			
	$r$	−0.27	+0.99	−0.28
	$p$ value	$p < 0.001$	$p < 0.001$	$p < 0.001$

$\alpha_{h,d}^k$  tree height  $h$ , versus tree diameter  $d$ ;  $\alpha_{csa,d}^k$  crown cross-sectional area  $csa$ , versus tree diameter  $d$ ;  $\alpha_{v,d}^k$  scaling of tree volume  $v$ , versus tree diameter  $d$ ;  $\alpha_{cv,v}^k$  crown volume  $cv$ , versus tree volume  $v$

( $n = 126$ ,  $p < 0.001$ ,  $r^2 = 0.13^*$ ,  $F_{1,124} = 18.71$ ) (not shown in the graph). Due to the counteracting signs of these three statistical relationships, the estimates of  $\alpha_{cv,v}$  show a narrower range compared to its individual components (e.g.  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ ) (Fig. 4, see the coefficients of variation in Appendix S8).

#### Comparison with scaling of the allometric ideal plant according to MST

While MST predicts  $\alpha_{h,d} = 0.66$  and  $\alpha_{csa,d} = 1.33$  (see solid vertical lines in Fig. 1), the total range across all species reaches from  $\alpha_{h,d} = 0.53 - 0.64$  and  $\alpha_{csa,d} = 1.15 - 1.63$  (Table 1), and underlines the difference between empirical observation and theoretical assumption. On average, Norway spruce achieves its growing space by more vertical and less lateral oriented crown expansion, while broadleaf trees like European beech and sessile oak behave inversely. In most cases, the CI limits do not comply with values predicted by MST (Table 1). While the observed values mostly exceed the predicted values in the

case of  $\alpha_{csa,d}$ , the opposite applies for  $\alpha_{h,d}$  and  $\alpha_{v,d}$ . The exponent  $\alpha_{cv,v}$  of the three species differ the least from  $\alpha_{cv,v} = 3/4$ , predicted by MST.

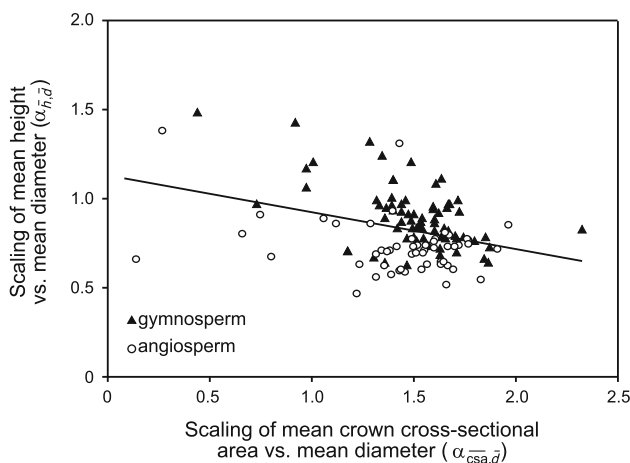
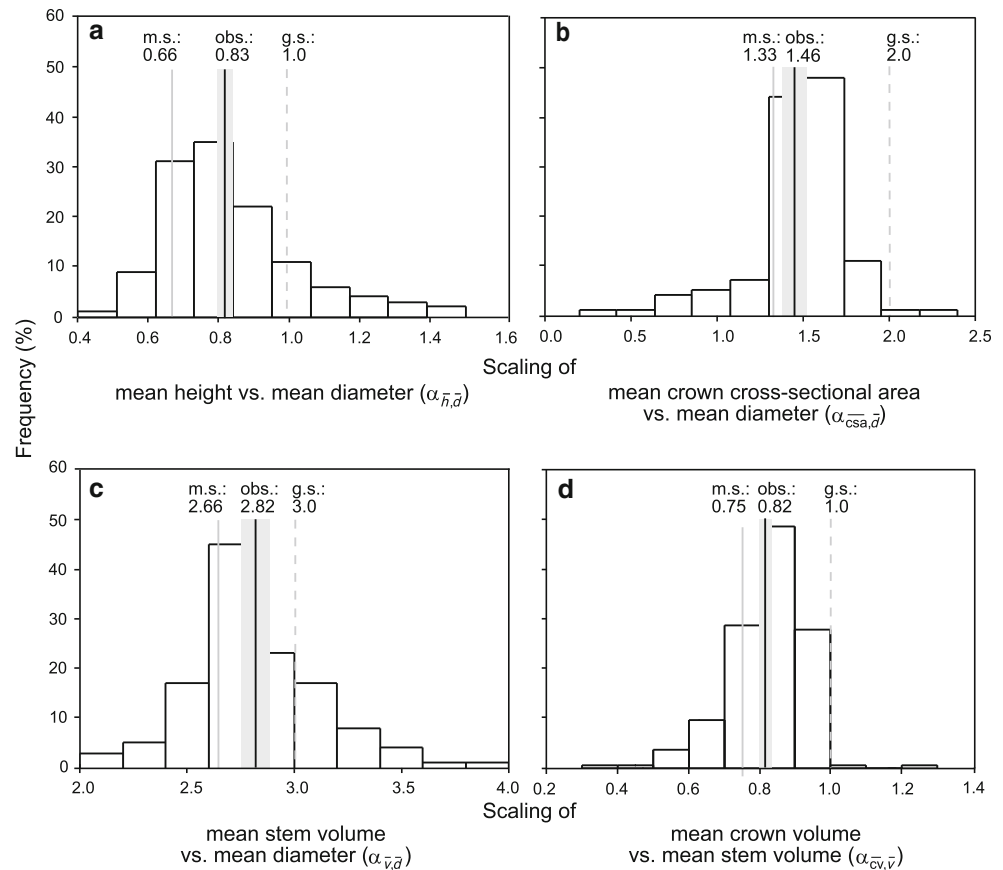
Analysis across 52 species indicates that the 95% CIs of the overall observed scaling exponents neither include scaling exponents predicted by MST (gray solid vertical line on the left) nor the exponents predicted by geometric similitude (broken vertical line on the right) (Fig. 4). Analogous to the pooled data, separate analysis of the scaling exponents of both species groups (30 angiosperm and 22 gymnosperm species) showed significant deviations from values predicted by MST for allometric ideal plants and also from Euclidian geometric scaling (Appendices S9 and S10). Though, exponents  $\alpha_{csa,d}$  and  $\alpha_{cv,v}$  are always closer to metabolic fractal scaling than to Euclidian geometric scaling.

#### Discussion

The following discussion of empirical findings on individual tree and stand level debunks the predictions of GST



**Fig. 4** Frequency distributions of observed scaling exponents  $\alpha_{\bar{h},\bar{d}}$ ,  $\alpha_{\bar{c}sa,\bar{d}}$ ,  $\alpha_{\bar{v},\bar{d}}$ , and  $\alpha_{\bar{c}v,\bar{v}}$  based on the yield table dataset (see Appendix S5). Expected scaling exponents for an allometric ideal plant (MST: *m.s.*) and for geometric similitude (GST: *g.s.*) are represented by gray vertical bars. The mean observed scaling exponents (*obs.*) are shown by black vertical bars. Gray bars around the observed values refer to the confidence limits (95% CI).  $\alpha_{\bar{h},\bar{d}}$ , scaling of mean height  $\bar{h}$ , versus mean tree diameter  $\bar{d}$ ;  $\alpha_{\bar{c}sa,\bar{d}}$ , mean crown cross-sectional area  $\bar{c}sa$ , versus mean tree diameter  $\bar{d}$ ;  $\alpha_{\bar{v},\bar{d}}$ , mean stem volume  $\bar{v}$ , versus mean tree diameter  $\bar{d}$ ;  $\alpha_{\bar{c}v,\bar{v}}$ , mean crown volume  $\bar{c}v$ , versus mean stem volume  $\bar{v}$



**Fig. 5** Negative relationship between scaling exponents  $\alpha_{\bar{h},\bar{d}}$  and  $\alpha_{\bar{c}sa,\bar{d}}$  across 52 tree species derived from 126 yield tables (Appendix S5). Shown are the observed values for gymnosperm (triangles) and angiosperm tree species (circles) as well as the straight line fitted through the pooled data by OLS regression.  $\alpha_{\bar{h},\bar{d}}$ , scaling of mean height  $\bar{h}$ , versus mean tree diameter  $\bar{d}$ ;  $\alpha_{\bar{c}sa,\bar{d}}$ , scaling of mean crown cross-sectional area  $\bar{c}sa$ , versus mean tree diameter  $\bar{d}$

and MST concerning structural allometry as an overgeneralization. Zeide (1987, 1998), Pretzsch and Schütze (2005), Pretzsch (2006), Price et al. (2009) and Duursma

et al. (2010) have already stressed that structural allometry is variable rather than constant. This study, however, goes beyond a simple falsification. It analyzes, as prompted by Price et al. (2010), to what extent different allometric exponent deviate from MST, correlate with each other, and interact. Variability of allometric scaling and fractal space filling are revealed as prerequisite for the individual plant's competitiveness and stable scaling.

#### Intra-individual versus inter-individual allometry

Most of the mentioned studies are based on inter-individual or inter-stand datasets gathered on the plant or stand level at one point in time (e.g., West et al. 1997; Enquist and Niklas 2001; West et al. 2009). The reason why this is a common approach especially in grassland science and agronomy is that herbaceous plants are very difficult to trace in their individual allometric growth by repeated measurements without causing artefacts due to disturbing the stand and plant structure by repeated surveys. So, records of differently sized plants in a stand at the same time are used as substitute for the missing real time series (Weiner and Thomas 1992; Weiner 2004). In view of the longevity of forest stands, effects of environmental changes, disturbances like wind-throw, ice-breakage, or insect

calamities, which are not always documented, may often be hidden in the given stand structure. Thus, a composed artificial time series reflects rather the result of disturbances and adaptation than the size-dependent allometric trajectory expected under undisturbed conditions. In order to avoid such common flaws, we used repeated long-term measurements on the tree and stand level which better reveal the change of structure with size growth. Effects of auto-correlation due to successive measurements of the same plant were eliminated by application of linear mixed effect models for statistical analysis (see “Materials and methods”). Divergences between our intra-individual or intra-stand analyses and results of other studies might reflect the difference between the real time series we analyzed, and the results from artificial time series compiled in most other works. For instance, the relationship between plant diameter and height, when derived from inter-individual data (artificial time series), can be considerably flattened by subdominant plants that enhance their height growth at the expense of their diameter growth in order to stay in the game (Weiner 2004).

Deviation from both, metabolic and geometric scaling theory

(1) For the allometry between tree height,  $h$ , and trunk diameter,  $d$ , MST predicts  $h \propto d^{2/3}$  and GST  $h \propto d$ . The analysis on individual tree level yielded for the species-specific means always  $\alpha_{h,d} < 0.66$  (Table 1). For the analysis on stand level (Fig. 4, Appendices S8–S10) applies  $\alpha_{h,d} > 0.66$  but  $\alpha_{h,d} < 1.0$ .

(2) Contrary to the predicted scaling of crown cross-sectional area,  $csa$ , versus diameter,  $d$ , (MST predicts  $csa \propto d^{4/3}$ , GST  $csa \propto d^2$ ) observation on individual tree level are always lower than 2.0, and in the case of beech even lower than 4/3. The 95% CI include neither GST nor MST predictions. At the mean tree level  $\alpha_{csa,d} = 1.458 \pm 0.030$  includes neither GST nor MST predictions, merely the 95% CI for the angiosperms includes 4/3 (Appendix S10).

(3) Between total volume,  $v$ , and tree diameter,  $d$ , (MST predicts  $v \propto d^{8/3}$ , GST  $v \propto d^3$ ),  $\alpha_{v,d}$  mean values at individual tree level lie always below 8/3. On mean tree level, most  $\alpha_{v,d}$  lie between 2.67 and 3.0 but the 95% CI includes neither. One exception is the group of angiosperms, where  $\alpha_{v,d} = 2.732 \pm 0.054$  (Appendix S10) includes 8/3.

(4) The analysis of the relationships between crown volume,  $cv$ , and total tree volume,  $v$ , (MST predicts  $cv \propto v^{3/4}$ , GST  $cv \propto v$ ) yielded for beech on individual tree level correspondence with MST. However, in all other cases  $\alpha_{cv,v}$  is greater than 3/4 but less than 1.0. Also  $\alpha_{cv,v}$  extracted from the yield table data with

$\alpha_{cv,v} = 0.817 \pm 0.011$  for all species,  $0.837 \pm 0.012$  for the gymnosperms and  $0.791 \pm 0.091$  for the angiosperms exceeds the prediction by MST but is below the prediction by GST (see Appendices S8–S10).

With respect to  $\alpha_{cv,v}$ , it should be considered that crown length may not be proportional—as was assumed based on McMahon and Kronauer (1976)—but decreases with size growth, such that  $cl \propto h^{\alpha_{cl,h}}$  with  $\alpha_{cl,h} < 1$ . This in turn would imply a slight reduction of the slope  $\alpha_{cv,v}$ , as the crown volume was calculated from  $csa \times h$ . Specific wood density  $R$  was assumed not to change with plant size ( $R = m/v \cong \text{const.}$ ), such that  $m \propto v$  and mass is proportional to volume in the aforementioned relationships. For selected tree species, Knigge and Schulz (1966) shows that  $R$  may be coupled to tree ring width and can either increase (broadleaf trees) or decrease (conifers) with size and make the slopes of scaling with mass shallower or steeper, respectively, in comparison to scaling with tree volume. In addition, all scaling approaches dependent on either tree mass or tree volume are biased, as long as they do not take into consideration that much of the tree stem actually consists of physiologically inactive heartwood (Pretzsch 2010). Most of the discussed error sources result in a slight overestimation of the scaling exponents, such that a correction (for which appropriate data are lacking) would reduce them. However, the majority of results on tree as well as on stand level deviate to such a considerable extent from MST, as well as from GST, that both generalizations simply do not match biological observation.

Variable rather than stable allometry

Within a broad range, competition can squeeze or stretch the crown and cause the observed broad intra-specific variation in scaling of structure (Figs. 1, 2). Constant morphological scaling as assumed by West et al. (1997, 2009) may be useful as a first assumption. It enables a simple transition from plant metabolism via plant structure to space occupation and population dynamics. However, in view of the morphological plasticity found by many studies (Duursma et al. 2010; Kolokotronis et al. 2010; Pretzsch 2010; Price et al. 2009), quantification of the variation and covariation of structural traits within species, between species and over time seems more promising than to assume constant scaling equivalent to metabolic 3/4 scaling.

Our results provide evidence for both (1) variability in intra-specific scaling also pointed out by Dodds et al. (2001) and Kolokotronis et al. (2010), and (2) inter-specific variation suggested by Price et al. (2009, 2010). Firstly, obviously there is a close covariation between the different exponents of structural allometry; for instance, a

negative correlation between vertical and lateral crown expansion (Fig. 3). For Norway spruce, European beech, and sessile oak applies a negative correlation between  $\alpha_{h,d}$  and  $\alpha_{csa,d}$  as well as between  $\alpha_{csa,d}$  and  $\alpha_{v,d}$ . In contrast  $\alpha_{h,d}$  and  $\alpha_{v,d}$  correlate positively. In the “Introduction”, we separated  $\alpha_{cv,v}$  into three components  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ , and  $\alpha_{v,d}$  and showed that  $\alpha_{cv,v} = (\alpha_{h,d} + \alpha_{csa,d})/\alpha_{v,d}$ . The correlation between the components contributes to a stabilization of  $\alpha_{cv,v}$  on a species-specific level. This underlines that any deviations of this components from scaling predicted by GST or MST is not inevitably a contradiction to their core assumption (MST  $cv \propto v^{3/4}$ , GST  $cv \propto v$ ) as the interaction between the components of crown structure scaling may yield 3/4 or 1.0. On the other hand, when components of the crown allometry (e.g.  $\alpha_{h,d}$  or  $\alpha_{v,d}$ ) correspond with MST or GST that does not indicate inevitably that the scaling on whole tree level corresponds as well, because covariation between these allometric relationships can cancel, compensate, or enhance the scaling on tree level. Secondly, the yield table data confirmed inter-specific differences in crown scaling also found by Zeide (1985), von Gadow (1986), Weller (1987), and Pretzsch and Biber (2005). Our results signify a departure from general scaling of structure and from the concept of an allometric ideal plant. However, the stand level allometry derived from the yield tables also reveals a trade-off between vertical and lateral structural extension. Analogous to the intra-specific variability, we find an inter-specific correlation between  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ , and  $\alpha_{v,d}$  which does not keep  $\alpha_{cv,v}$  constant at 3/4, but stabilizes it in a quite narrow corridor around 3/4. In view of this variability, scaling of the allometric ideal plant may be of benefit when using it as reference but is somewhat of a phantom when trying to find it. With respect to crown structure, a more detailed scrutiny of its various components with special focus on their interactions and combined effect appears more promising than to continue the endless alternation between complete rejection and enthusiastic approval of overarching scaling laws. Stable metabolic scaling and variable scaling of crown and root structure are not necessarily a contradiction. It is rather this variability of the crown which provides a plastic holding structure for the leaf organs and enables the plant to keep close to the 3/4 power leaf mass–plant biomass trajectory. According to that, morphological variability is even a requirement for holding trees on a rather stable leaf mass–plant mass or root mass–plant mass trajectory even under variable or changing environmental conditions.

#### Fractal-like crown space filling principles

The leaf mass–plant mass allometry can be assumed to follow generally 3/4 scaling (West et al. 1997; Niklas

2004). MST further assumes that the crown volume–plant volume allometry also follows 3/4 scaling as  $cv \propto ml$  and  $v \propto mt$  (West et al. 2009). That means  $cv \propto v^{3/4}$  is the structural analogue to the metabolic scaling  $ml \propto mt^{3/4}$ . However, our results show a considerable intra- and inter-specific variation of  $\alpha_{cv,v}$  due to a broad variation and covariation of its components  $\alpha_{h,d}$ ,  $\alpha_{csa,d}$ , and  $\alpha_{v,d}$  (Figs. 1 and 4). According to the rather well-backed core assumption of MST, an increase of tree volume or mass of 1% is always coupled with an 3/4% increase of leaf mass, while it can be coupled with an increase of crown volume between  $\alpha_{cv,v} = 0.77$ – $0.82\%$  (according to the means of the three species in Table 1) or  $0.796$ – $0.839\%$  (according to the 95% CIs for the 52 species in Fig. 4d). This finding is contradictory to Osawa (1995) who assumes  $cv \propto v$  and West et al. (2009) who assume generally  $\alpha_{cv,v} = 3/4$  (e.g.,  $cv \propto v^{3/4}$ ). This deviation indicates the following important species-specific and variable space-filling principle of the crown volume by leaves depending on the fractal surface dimension.

When the crown is modelled as an Euclidian body without indentations (following the wrapping approach by Christo and Jeanne-Claude, see <http://www.christojeanneclaude.net/wt.shtml>) and  $l$  is its diameter, then the crown volume is  $cv \propto l^3$  and the crown surface area  $cs \propto l^2$ . For the leaf area applies the same only if all the leaves are allocated close to the convex hull. According to fractal geometry, leaf area scales as  $la \propto l^n$ , with surface dimension  $n = 2$ – $3$  (Hutchinson 1981; Mandelbrot 1983). Tree crowns as described by Oldemann (1990), Roloff (2001) and Purves et al. (2007) lie somewhere in the continuum between the borderline cases of an umbrella-like crown with the whole leaf surface area allocated close to the convex hull ( $n = 2$ ) and a broom-like crown with leaf surface area distributed all over the crown space ( $n = 3$ ) (Zeide 1998). From  $cv \propto l^3$  and  $la \propto l^n$  results  $la \propto cv^{n/3}$ , and insertion of  $la \propto mt^{3/4}$  yields.

$$cv \propto v^{3/4 \times 3/n} \quad (3)$$

as we can assume  $mt \propto v$  (as  $mt = v \times R$ ,  $R$  = specific wood density). Equation 3 combines the general 3/4 scaling of metabolism with the  $n$ -dimensional fractal scaling of crown surface structure. The theoretical results of  $\alpha_{cv,v} = 1.125$  for umbrella-like crowns (insertion of  $n = 2$  into Eq. (3)) and  $\alpha_{cv,v} = 0.75$  for broom-like crowns ( $n = 3$ ) corresponds well to the range of our observed scaling exponents (Table 1; Fig. 4d).

Metabolic 3/4 scaling theory assumes that the fractal like surface area of all of the leaves and crown volume scale are identical ( $la \propto cv$ ), in other words, always  $n = 3$  (West et al. 2009). In contrast, 2/3 power Euclidian relationships assumed in general ( $la \propto cv^{2/3}$ ) that means  $n = 2$

(Rubner 1931; von Bertalanffy 1951). Equation 3 provides an approach for estimating the fractal dimension  $n$  depending on crown volume and tree volume as  $\alpha_{cv,v} = 9/4 n$  and  $n = 9/4 \alpha_{cv,v}$ . If we insert mean values and 95% CI limits of  $\alpha_{cv,v}$  from Table 1 into Equation  $n = 9/4 \alpha_{cv,v}$ , we receive  $n = 2.81$  and  $n = 2.74$ – $2.85$  for Norway spruce and  $n = 2.92$  and  $n = 2.81$ – $3.00$  for European beech, and  $n = 2.74$  and  $n = 2.71$ – $2.78$  for sessile oak. Insertion of the mean values and 95% CIs across the 52 species result in  $n = 2.75$  and  $n = 2.68$ – $2.83$ . This range of  $n$  values contradicts overarching structural scaling assumptions by MST but corresponds with results by Osawa (1995) and Zeide (1998) who found a considerable intra- and inter-specific variation of the fractal dimension  $n$  and a dependency from the tree's social rank and the species.

For analyses and derivations in this study, we assumed like West et al. 1997 and Enquist and Niklas 2001 that leaf area is proportional to leaf mass ( $la \propto ml$ ). Thorough analysis by Niklas et al. (2009) and Price et al. (2010) question the proportionality between leaf area and leaf mass. However, as the deviations from proportionality are rather small and not yet sufficiently substantiated, we temporarily assumed  $la \propto ml$ . A consolidated view shows numerous studies which find in accordance to the MST for many species the same relative increase in leaf mass or leaf area of  $3/4$  when growing in size ( $ml \propto mt^{3/4}$  and  $la \propto mt^{3/4}$ , respectively). However, contrary to MST, those species which arrange their leaf area in an umbrella-like shape are more space demanding compared with trees with broom-like crowns. We conclude that observed developments of plant structure seem to result from both a general metabolic allometry and partitioning, which is inherent in all woody and herbaceous plant species, and a species-specific structural allometry and variability in structure and space filling which reflects an adaptation and acclimation to selective pressure (Weiner 2004; McCarthy and Enquist 2007).

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